Breakdown and invertebrate colonisation of kamahi leaves in southern New Zealand streams

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(Received 5 December 2006, revised and accepted 2 February 2007)

Abstract

The contribution of invertebrates to weight loss of kamahi leaves incubated in "coarse-mesh" (7 mm) and "fine-mesh" (0.2 mm) bags was investigated in 10 southern New Zealand streams (South Westland and Stewart Island) with a wide range of water pH. Coarse-mesh bags containing plastic strips as leaf analogues were also deployed in the four South Westland streams. Leaves lost up to 22-45% of initial dry mass after 54-62 days, with subsequent losses showing considerable variation among sites and bag mesh sizes. The difference between mass loss in coarse-mesh compared to fine-mesh bags typically increased over time, indicating that invertebrate feeding had a greater role in leaf breakdown as leaves became more conditioned. ANOVA indicated significant differences among sites and bag mesh sizes in leaf decay, but a non-significant effect of region (Stewart Island versus South Westland). Exponential decay coefficients ($-k$ day^{-1}) calculated for all sites after 122-133 days were strongly related to water pH in coarse-mesh but not fine-mesh bags, suggesting that pH-mediated effects on leaf breakdown operated directly or indirectly on invertebrate rather than microbial activity. Although region did not affect leaf decay, it did have an influence on the structure and composition of invertebrate communities colonising bags. In Westland, invertebrate communities in coarse-mesh bags reflected water pH rather than whether bag contents were leaves or plastic strips. Our results indicate that the rate of leaf breakdown from a single tree species varied widely among sites, reflecting site-specific variations in the pool of colonising invertebrates and natural water chemistry. This finding emphasises the need to select appropriate reference sites for studies intending to use leaf decay rates as functional indicators of the health of streams subject to anthropogenic stressors.

Keywords: leaf decomposition - *Weinmannia racemosa* - invertebrate feeding - functional indicators - Stewart Island - Westland.

Introduction

Early New Zealand studies of leaf decomposition focussed on the breakdown of beech (*Nothofagus*) leaves in Canterbury streams (Davis & Winterbourn 1977; Winterbourn 1978; McCammon 1980; Rounick & Winterbourn 1983), and the role of terrestrial organic matter inputs in sustaining stream invertebrate communities. These studies were pivotal in (i) determining the significance of allochthonous inputs in New Zealand forest stream food webs, and (ii) formulating hypotheses on why New Zealand invertebrate faunas apparently did not conform to patterns predicted by the River Continuum Concept (Vannote *et al.* 1980). The paucity of native deciduous tree species and poor retentive capacity of streams with highly variable flow regimes were thought to contribute to the paucity of stream invertebrate communities centred on the direct utilisation of coarse particulate organic matter (Winterbourn *et al.* 1981).

In the wake of these early New Zealand studies, interest expanded into the decomposition dynamics of leaves from other tree species, including willow (*Salix babylonica*), fuchsia (*Fuchsia excorticata*), red beech (*Nothofagus fusca*) and mahoe (*Melicytus ramiflorus*) (Collier & Winterbourn 1986; Linklater 1995), and included a comparison of breakdown and colonisation of leaves belonging to several native and introduced tree species (Parkyn & Winterbourn 1997). Other research focussed on the effects of environmental stressors such as low pH on leaf breakdown rates (e.g., Collier & Winterbourn 1987a), stimulated by overseas studies on the effects of anthropogenically-derived acidic deposition (Hildrew *et al.* 1984; Burton *et al.* 1985; Allard & Moreau 1986).

Leaf decomposition studies are undergoing a renaissance in stream ecology, both in New Zealand and overseas, as interest grows in the use of functional indicators to assess ecological health (or integrity) of streams (e.g., Robinson & Jolidon 2005; Young 2005). To interpret leaf breakdown patterns observed at impacted sites, it is important to understand factors affecting decomposition rates under natural conditions. What are the relative contributions of invertebrate and microbial activity to leaf breakdown, and how are they affected by natural variations in background physico-chemical conditions? The present study describes the breakdown of leaves from a widespread native tree species, kamahi (*Weinmannia racemosa*), in 10 pristine streams in Westland and on Stewart Island, southern New Zealand. The streams had a wide range of water pH ranging from highly acidic to slightly alkaline. The aims of this synthesis are to: (i) assess the effects of location at two spatial scales (region and site) on leaf breakdown rates relative to water chemistry and invertebrate colonisation, and (ii) compare breakdown rates in these contrasting streams with those of other native leaf species to provide a broad understanding of the variability present under reference site conditions.

Methods

Study area

Leaf bags were deployed at four sites in South Westland, and six sites on Stewart Island in southern New Zealand. The Westland sites were within 22 km of each other and comprised two circum-neutral, clear-water sites (Hidden Creek and Toilet Stream) and two acidic, brown-water sites (Steep Creek and Suspect Stream) that contained high concentrations of dissolved organic carbon (see Collier & Winterbourn 1987b for details of water chemistry; see also Table 1). Both brown-water streams were about 2.5 m wide at the study sites and drained pakahi wetlands. Riparian vegetation was podocarp forest (including kamahi) and manuka (*Leptospermum scoparium*). The clear-water sites were also on small streams (about 1.4 m wide) that flowed into Waiho River in the Franz Josef Glacier valley. Water temperature ranged from 5 to 17 °C at Steep, Suspect and Toilet streams, but was less variable at spring-fed Hidden Creek (8-12 °C).

The Stewart Island sites were on tributaries and main branches of the Rakeahua River (catchment area 106 km^2), the largest river on the island (Chadderton 1990). All sites were on slightly acidic brown-water streams with pH values between those of the two pairs of Westland sites (Table 1). Sites 1 and 2 were on small (1.5-2.0 m channel width), stony-bottomed streams draining podocarp forest dominated by rimu (*Dacrydium cupressinum*) and kamahi. Site 3 was on a slightly larger (3^{rd} order, 2-3 m wide) stony stream that also drained podocarp forest. Sites 4, 5 and 6 were moderately wide (6-10 m) and were located on deep, sluggish, meandering sections of the two main branches of the river. Substrata at these sites were coarse sand and woody debris, including whole manuka trees that had collapsed into the river. Riparian vegetation was tall manuka scrub with an understorey of small *Coprosma* shrubs, pepperwood (*Pseudowintera collorata*) and grasses (*Microlaena avenacea*, *Uncinia uncinata*, *Carex geminata*). Water temperature was 6-10 °C at Site 1, 1.5-14 °C at Site 2, and 4.5-15 °C downstream of sites 4, 5 and 6, during the study.

Leaf bags

Green leaves were collected from kamahi trees in each of the study areas, and 5-10 g of leaf material were placed in "coarse-mesh bags" (7 mm mesh, 15 cm long x 14 cm wide) to provide free access to all invertebrates, and "fine-mesh bags" (10 cm long x 4 cm diameter PVC tubes covered at both ends by 0.2 mm mesh) to restrict access to invertebrates but still

Table 1. Mean stream water pH, dissolved organic carbon (DOC) and alkalinity values (ranges in parentheses) for the 10 study sites sampled on 4-6 occasions.

	pH	DOC g m^{-3}	Alkalinity g m^{-3} $CaCO_3$
Westland			
Hidden	7.5 (6.6-8.0)	0.8 (0.4-1.2)	49.0 (40-56)
Toilet	7.4 (7.2-7.7)	1.4 (0.6-4.2)	42.6 (12-54)
Steep	4.9 (4.2-5.7)	8.9 (6.3-12.5)	0.4 (0.2-1.2)
Suspect	4.6 (4.2-4.9)	12.1 (8.7-15.5)	0.4 (0.2-1.0)
Stewart Island			
S1	6.8 (6.4-7.0)	6.3 (4.9-9.7)	12.9 (6.9-16.5)
S2	6.6 (6.2-6.9)	7.3 (5.9-10.9)	6.7 (3.7-10.0)
S3	6.4 (6.0-6.7)	9.2 (5.9-12.8)	11.0 (7.8-13.4)
S4	6.5 (5.9-6.8)	9.9 (7.0-15.9)	9.2 (4.9-14.2)
S5	6.6 (6.2-6.7)	8.4 (6.2-10.5)	11.1 (6.5-14.2)
S6	6.5 (6.1-6.8)	9.6 (6.6-15.5)	9.3 (4.9-12.5)

allow circulation of water over leaves (Rounick 1982). Leaf bags were then dried for 7 days at 50 °C. Dried leaves from 5-6 bags were reweighed to obtain a conversion factor for estimating initial leaf dry mass in each bag. Ten bags of each type were retained to determine any losses attributable to transport and storage, but such losses were negligible (typically <1%). Leaf bags were deployed in Westland streams for 54, 133 and 238 days (±1 day) during 1986, and in Stewart Island streams for 62, 122 and 220 days (±4 days) during 1989. Three replicates of each bag type were incubated for each period at all sites (i.e., a total of 90 fine-mesh and 90 coarse-mesh bags). Bags that were incubated for 238 days in Toilet and Suspect streams were lost following large floods.

Strips of black polyethylene (3 x 12 cm, n = 10 per bag) were also placed in sets of coarse-mesh bags at all Westland sites to act as inert leaf analogues that provided habitat but not a direct source of food for invertebrates. Following the removal of bags, leaves or plastic strips and associated invertebrates were either stored in 4-10% formalin (Stewart Island) or kept cool and frozen (Westland). Later, leaves were washed over a 150 µm-mesh sieve to remove invertebrates, which were identified and counted. The remaining washed leaf material was dried to constant weight at 50 °C and weighed (±0.1 mg).

Statistical analyses

Decay coefficients ($-k$ day^{-1}) were calculated for leaves after 122-133 days, when all replicate bags were retrieved successfully, using the exponential decay model of Petersen & Cummins (1974):

$$-k = \log_e (\%R/100)/t$$

where R = amount of leaf material remaining after t days in the stream.

Normality of data was investigated using probability plots and was deemed to be acceptable for parametric analysis. Analysis of variance (ANOVA) was performed on the percentage initial dry-weight remaining data (Datadesk 6.0) using region, site, bag mesh size and immersion time as factors. Non-metric multidimensional scaling (NMDS) (Primer 6.1.2) was conducted using percentage abundance invertebrate data (fourth-root transformed) and was followed by Analysis of Similarities (ANOSIM) to investigate differences among sites and regions, and among coarse-mesh bags containing leaves and plastic strips in Westland (all bags collected on any date combined). The fauna retrieved from leaf bags at Site 1 (Rakeahua Valley) after 220 days (S1-3) was identified as an outlier and excluded from the NMDS analysis.

Results

Leaf weight loss

Leaves in Westland streams lost an average of 27% (22-36%; all bags at any site combined) of initial dry weight in the first 54 days, but subsequent weight losses differed considerably between sites and bags of different mesh sizes (Appendix I). In the two highly acidic streams, very little additional leaf weight loss was recorded in any bags after day 54. Thus, 61-73% of initial mass remained after 238 days in Steep Creek, where leaves were still tough and yellow-green in colour, confirming that little microbial decomposition had occurred. No leaf bags were recovered from Suspect Stream on day 238, but after 133 days leaves in coarse-mesh bags had an average of 64% of initial mass remaining compared to 73% in fine-mesh bags. Only one coarse-mesh bag at alkaline, spring-fed, Hidden Creek had any leaf material left after 238 days, whereas 56% of initial leaf mass remained in fine-mesh bags indicating a marked effect of invertebrate feeding on leaf breakdown. In contrast, the less stable Toilet Stream had 44% initial mass remaining in coarse mesh bags on day 238. This represented a 4% loss from average weights recorded after 133 days, when leaves in fine-mesh bags had lost 71% of initial mass.

At the Stewart Island sites, leaves in coarse-mesh bags had lost 46% of initial mass by day 62 compared to 31% in fine-mesh bags (Table 2). After 122 days immersion, considerable skeletonisation of leaves was noted in coarse-mesh bags, whereas leaves in fine-mesh bags were intact and still tough. After 220 days, two groups of sites could be differentiated on the basis of leaf breakdown rates in coarse-mesh bags, with greater losses at Sites 1 and 2 (<10% initial dry mass remaining) than at Sites 3, 4, 5 and 6 (19-42%). The difference between breakdown rates in coarse-mesh compared to fine-mesh bags typically increased over time at Stewart Island sites, especially at Sites 1, 2, 4 and 5, and followed a similar pattern to that found at most Westland sites (Appendix I).

ANOVA confirmed there were significant differences in leaf decay rates among sites and bag mesh sizes, but that region (Stewart Island versus Westland) did not have a significant effect on leaf breakdown (Table 2). The interaction between region and mesh size was not significant, but it was for mesh size and site indicating differential effects of invertebrate feeding on leaf processing among streams. Immersion time also had a significant effect on decay rate and interacted significantly with mesh size and site. These results indicate there are complex interactions among site-specific factors, invertebrate feeding and temporal conditioning of leaves.

Exponential decay coefficients ($-k$ day^{-1}) calculated from weight loss data after 122-133 days are shown in Figure 1. Site ($F_{8,170}$ = 4.28, P <0.001) and mesh size of bags ($F_{1,170}$ = 99.60, P <0.001) had significant effects on decay coefficients, and a significant interaction was found between the two factors ($F_{8,170}$ = 4.38, P <0.001). Decay coefficients for leaves in coarse-mesh bags were positively related to stream water pH, but no such relationship

Table 2. Results of ANOVA comparing percentage initial dry weight remaining in relation to location (Stewart Island versus Westland), site (n = 10), mesh size (coarse- versus fine-mesh) and 3 immersion periods.

Source	df	MS	F	P
Location	1	2.85	0.05	0.818
Site	8	641.01	12.00	<0.001
Mesh	1	9704.28	181.70	<0.001
Location*Mesh	1	195.00	3.60	0.058
Site*Mesh	8	425.99	8.00	<0.001
Time	4	1059.29	19.80	<0.001
Site*Time	15	169.74	3.20	<0.001
Mesh*Time	4	789.65	14.80	<0.001
Error	128	53.40		
Total	170			

was found for leaves in fine-mesh bags (Figure 2).

Invertebrate communities

Fifty eight macroinvertebrate taxa were recorded in coarse-mesh bags taken from the 10 sites; 34 from the Westland bags and 38 from Stewart Island bags. Chironomidae was the most frequently encountered taxon (present in all 38 collections) followed by Oligochaeta (35), the leptophlebiid mayfly *Deleatidium*

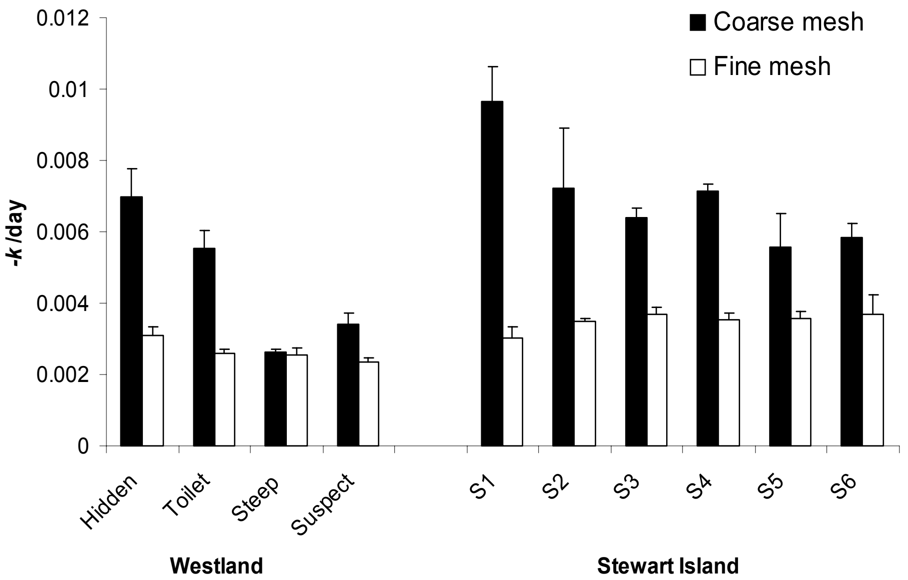

Figure 1. Mean (±1SE) decay coefficients (-*k* day^{-1}) for kamahi leaves incubated for 122-133 days in coarse-mesh (7 mm) and fine-mesh (0.2 mm) bags at 4 Westland and 6 Stewart Island (S1-S6) stream sites.

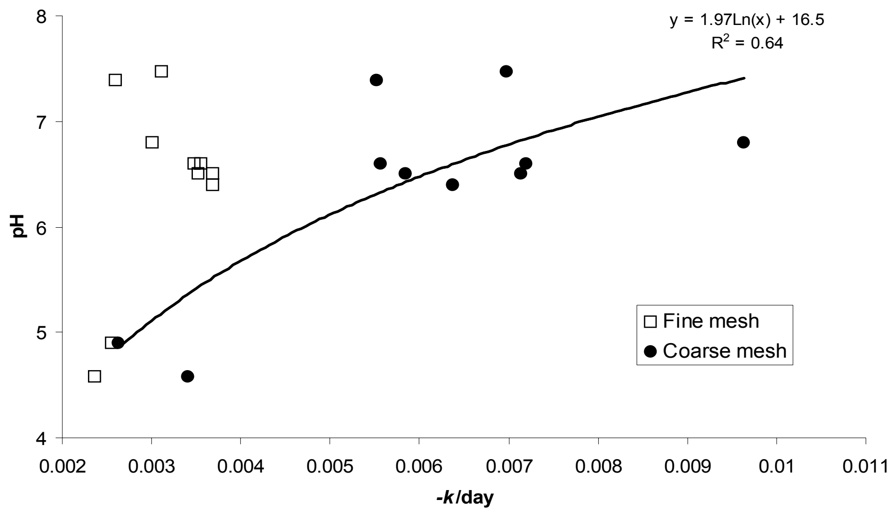

Figure 2. Relationship between mean stream water pH and decay coefficients (-*k* day^{-1}) for kamahi leaves incubated in coarse-mesh (7 mm) and fine-mesh (0.2 mm) bags at 10 sites.

(29), and (in 22-24 samples) Ceratopogonidae and Empididae (Diptera), and the stonefly *Austroperla cyrene*. Thirty taxa occurred at fewer than 5 sites. Chironomidae were relatively abundant in all coarse-mesh bags (20-89% of total numbers), followed by Crustacea (mainly amphipods and isopods) and Plecoptera (up to 38%) (Figure 3). Although invertebrates were also found in fine-mesh bags, they were predominantly small insect larvae, mostly Chironomidae, which would not have contributed significantly to leaf breakdown.

The NMDS analysis based on percentage abundance data showed groupings that reflected region (ANOSIM Global R = 0.712, P<0.001) (Figure 4A). Although ANOSIM indicated significant effects of site (Global R = 0.718, P <0.001) none of the pair-wise comparisons was statistically significant. Bags containing leaves or plastic strips in the South Westland streams were intermingled in two-dimensional ordination space (Figure 4B), with no statistical difference between the two kinds (Global R = -0.017, P >0.05). Rather, the South Westland groupings reflected site (Global R = 0.763, P <0.001), with all pair-wise site differences significant, except between Steep Creek and Suspect Stream collections.

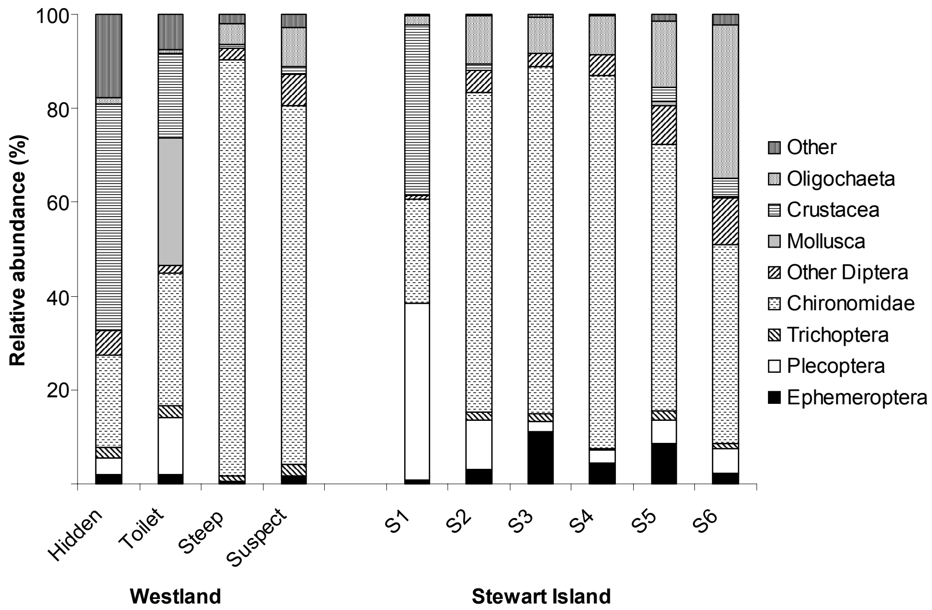

Figure 3. Percentage abundance of major invertebrate groups in coarse-mesh bags at 4 Westland and 6 Stewart Island (S1-S6) stream sites (all dates combined).

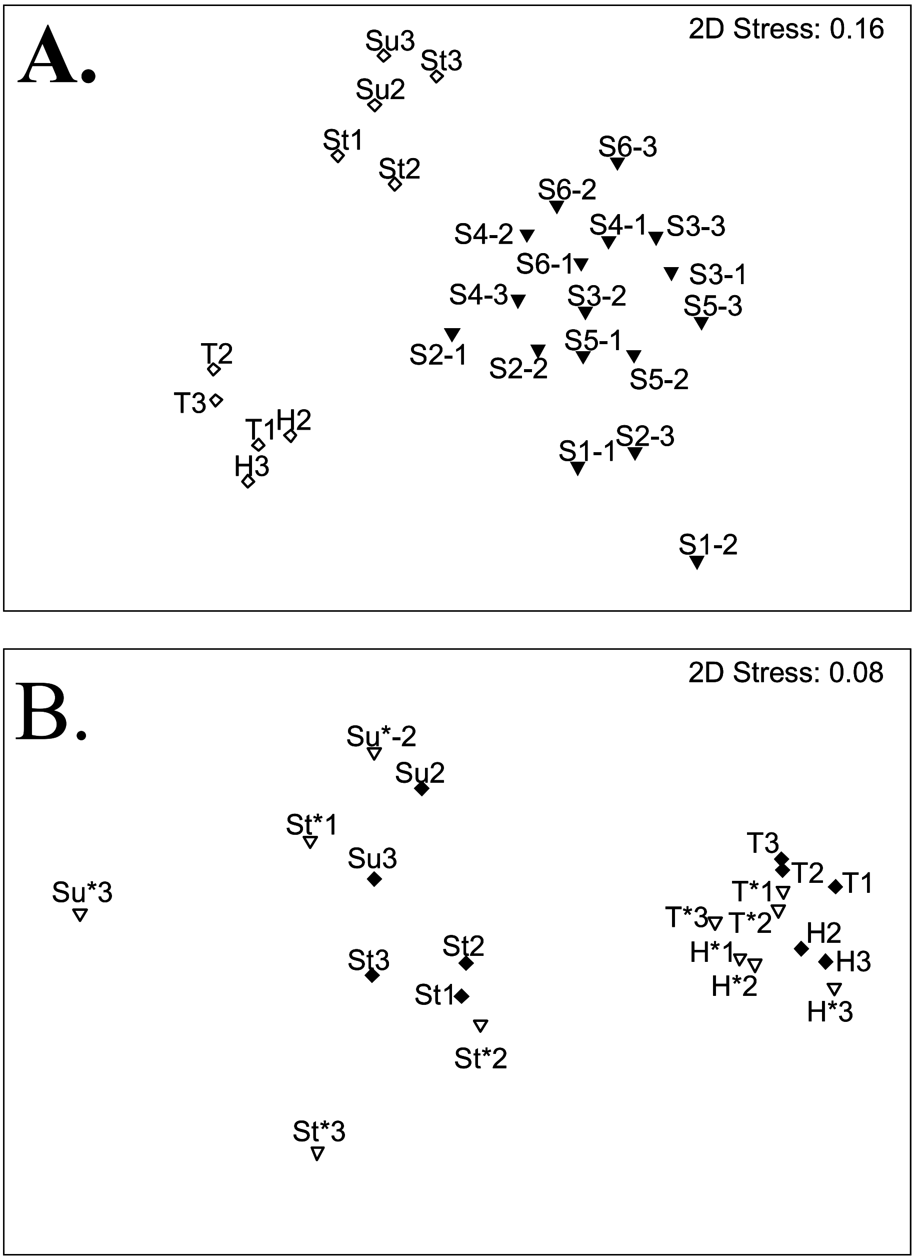

Figure 4. Non-metric multidimensional scaling plots of percentage abundance invertebrate data from coarse-mesh bags containing (A) kamahi leaves incubated for up to three dates at 10 sites, and (B) leaves or plastic strips at 4 Westland sites. H = Hidden, T = Toilet, St = Steep, Su = Suspect; S = Stewart Island sites (S1-S6). Numbers following site codes indicate sequence of immersion periods. In B, * = plastic strips.

Discussion

Information on organic matter breakdown rates at reference sites is important for interpreting the results of functional indicator studies aimed at quantifying anthropogenic impacts on lotic ecosystem processes. For example, Paul *et al.* (2006) reported slower decay rates of maple (*Acer barbatum*) leaves at forested sites than in agricultural, suburban or urban streams in the south-eastern United States. However, only a few studies in New Zealand have investigated leaf breakdown rates in native forest streams. In two of the most comprehensive studies, kamahi leaves broke down more slowly (t_{50} >80 days) than leaves of *Fuchsia exorticata*, *Melicytus ramiflorus* and *Nothofagus fusca* kept in coarse-mesh (5 mm) bags at Cass (Parkyn & Winterbourn 1997) and on Banks Peninsula (Linklater 1995) where water temperatures were between 7 and 15 °C. Furthermore, decay coefficients for kamahi leaves incubated at highly acidic Westland sites (Collier & Winterbourn 1987a; this study) were amongst the slowest recorded in native forest streams in the South Island, and comparable to those recorded by Rounick & Winterbourn (1983) for slow-decomposing mountain beech leaves (Table 3).

Regional differences in breakdown rates were evident in the present study, with decay rates typically being faster in both coarse-mesh (up to 3.7 times faster) and fine-mesh (up to 1.6 times faster) bags incubated in Stewart Island streams. This finding suggests there were either marked differences in microbial and invertebrate activity in leaf bags in the two regions, or that differences in experimental protocols or timing of the two studies affected decay rates, or that kamahi leaves sourced from different regions differed in their susceptibility to decay. With respect to the latter point, it may be significant that dry weight: fresh weight ratios were higher for Westland leaves (1: 2.6) than Stewart Island leaves (1: 2.2).

Although stream water pH accounted for 64% of the variation in leaf decay coefficients in coarse-mesh bags at the ten sites, the relationship was driven principally by the two highly acidic Westland sites and there was considerable variation in decay rates among sites with pH >6. In contrast, no relationship was found between pH and decay coefficients for leaves in fine-mesh bags in the ten streams. Furthermore, reductions in leaf dry mass were up to 74% higher in coarse-mesh than fine-mesh bags, with the difference between them typically increasing over time. This suggests that leaves become more attractive to invertebrates as they get older possibly because microbial conditioning increases over time and makes leaves increasingly attractive as food. The slower breakdown of leaves at the most acidic sites may also reflect a lesser degree of conditioning at low pH, and is supported by results of a food choice experiment with the leaf-feeding stonefly *Austroperla cyrene* (Collier 1988). Thus, nymphs of this shredder preferred leaves from circum-neutral Hidden Creek over leaves from acidic Steep Creek where respiration rates of leaf-colonising microflora were lower and by inference leaves were more weakly conditioned.

In the various streams, shredders included larvae of *Austroperla cyrene, Olinga feredayi, Oeconesus maori, Triplectides* sp., and tentatively, *Spaniocerca* spp., all of which were found on mountain beech leaves by Davis &

Table 3. Details of leaf breakdown studies (in order of increasing $-k$ day^{-1} values) that allowed access to most invertebrates (i.e., $\geq$3 mm mesh) to native tree leaves submerged in South Island streams draining catchments of native forest or subalpine scrub. ND = no data. Regions are in parentheses after Stream/site; SW = South Westland, IC = Inland Canterbury, SI = Stewart Island, and BP = Banks Peninsula.

Tree species	Common name	Stream/site	Mesh size (mm)	Max. days in stream	$-k$ day^{-1}
Weinmannia racemosa	Kamahi	Steep (SW)	7	238	0.0026 [(1)]
Nothofagus solandri var. *cliffortioides*	Mountain beech	Craigieburn Cutting (IC)	3	154	0.0028 [(2)]
W. racemosa	Kamahi	Suspect (SW)	7	230	0.0034 [(1)]
N. solandri var. *cliffortioides*	Mountain beech	Middle Bush (IC)	10	95	0.0055 [(3)]
W. racemosa	Kamahi	Toilet (SW)	7	238	0.0055 [(1)]
W. racemosa	"	S5 (SI)	7	220	0.0056 [(1)]
W. racemosa	"	S6 (SI)	7	220	0.0058 [(1)]
W. racemosa	"	S3 (SI)	7	220	0.0064 [(1)]
W. racemosa	"	Hidden (SW)	7	238	0.0070 [(1)]
W. racemosa	"	S4 (SI)	7	220	0.0071 [(1)]
W. racemosa	"	S2 (SI)	7	220	0.0072 [(1)]
W. racemosa	"	S1 (SI)	7	220	0.0096 [(1)]
Melicytus ramiflorus	Mahoe	Middle Bush (IC)	10	95	0.0135 [(3)]
Fuchsia exorticata	Fuchsia	Fuchsia (BP)	5	ND	0.0164 [(4)]
Nothofagus fusca	Red beech	Tawai (BP)	5	ND	0.0186 [(4)]
N. fusca	"	Middle Bush (IC)	10	95	0.0225 [(3)]
N. solandri var. *cliffortioides*	Mountain beech	Middle Bush (IC)	3	154	0.0267 [(2)]

[1] This study
[2] Rounick & Winterbourn (1983)
[3] Parkyn & Winterbourn (1997)
[4] Linklater (1995)

Winterbourn (1977). The snail *Potamopyrgus antipodarum*, which was abundant at one of the Westland sites (Toilet Stream), can also contribute to leaf breakdown by rasping the surfaces of leaves (Collier & Winterbourn 1986), and the omnivorous isopod *Austridotea lacustris f*eeds on leaf material as well as wood and invertebrates, which dominated gut contents of individuals collected from Stewart Island streams (Chadderton *et al.* 2003). It is conceivable that predation by *A. lacustris* may have reduced the numbers of invertebrates feeding in bags at sites S5 and S6 where it was common and where leaf breakdown rates were the lowest recorded on the island.

Finally, we return to the initial question posed regarding the relevance of our findings to the recent upsurge in interest in the use of leaf decomposition as a functional indicator of stream health. If regional or temporal differences in leaf phenology affect decay rates, then it is important to source leaves from the same place and season when making comparisons among sites or studies. Our results suggest there can be wide variation in leaf breakdown rates among undisturbed sites and that they potentially reflect site-specific variations in the pool of colonising invertebrates, and . the natural chemistry of the water. Our findings therefore reinforce the importance of selecting appropriate reference sites when it is intended to use leaf decay rates as functional indicators of stream health.

Acknowledgements

Kevin Collier's research was supported by the New Zealand Forest Service and NWASCA, and Lindsay Chadderton received financial assistance from the Department of Conservation, Royal Forest & Bird Protection Society of New Zealand, and the New Zealand Lotteries Board. We thank Ron Tindall and his team for logistic support on Stewart Island, the New Zealand Forest Service for use of the hut at The Forks, South Westland, and Ann Graesser, Malcolm Main, Richard Allibone, Jon Harding and Jen Tank, amongst others, for valuable help in the field.

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Appendix I. Percentage initial dry weight remaining of kamahi leaves incubated for up to 3 periods in coarse-mesh (7 mm) and fine-mesh (0.2 mm) bags at 10 sites, and the difference in weight of material in coarse- and fine-mesh bags.

	Days in stream	Coarse-mesh Mean	Coarse-mesh SE	Fine-mesh Mean	Fine-mesh SE	Difference in means
Westland						
Hidden	54	63.7	1.4	75.4	0.4	11.7
	133	40.0	4.3	66.1	2.1	26.1
	238	13.9	13.9	56.4	11.8	42.5
Toilet	54	69.9	1.1	77.8	0.4	7.9
	133	48.2	3.4	70.8	1.2	22.7
	238	44.0	13.2	Lost	Lost	-
Steep	54	70.3	2.2	78.0	1.2	7.7
	133	70.4	0.7	71.2	1.7	0.8
	238	61.3	2.1	73.2	1.3	11.9
Suspect	54	71.8	1.2	76.0	2.0	4.2
	133	63.6	2.7	73.0	1.1	9.4
	238	Lost	Lost	Lost	Lost	-
Stewart Island						
S1	62	60.1	2.1	80.3	1.7	20.2
	122	31.3	3.7	69.4	2.8	38.0
	220	1.2	0.3	63.8	1.8	62.5
S2	62	64.8	2.3	73.3	1.3	8.5
	122	43.3	8.6	65.4	0.7	22.1
	220	9.1	5.2	60.0	2.9	50.9
S3	62	60.8	3.3	73.7	0.2	12.9
	122	46.0	1.5	63.8	1.6	17.8
	220	41.5	5.1	58.6	2.0	17.1
S4	62	59.4	2.8	69.4	1.3	10.0
	122	41.9	1.0	65.1	1.8	23.2
	220	19.4	1.3	54.8	1.5	35.4
S5	62	64.4	4.1	71.6	2.8	7.2
	122	51.4	5.6	64.8	1.7	13.5
	220	30.4	2.3	57.4	2.0	27.0
S6	62	63.7	0.4	70.4	3.6	6.7
	122	49.1	2.5	64.0	4.1	14.9
	220	41.8	0.5	56.3	1.1	14.6